Effect of avalanche frequency on forest ecosystem services in a spruce-fir mountain forest

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Highlights

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Effect of avalanche frequency on forest ecosystem services in a spruce–fir mountain forest

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- We quantified ecosystem services in a spruce–fir forest under variable avalanche frequency.
- The avalanche track had higher plant diversity and lower carbon (C) stocks.
- 50 years after disturbance, the forest was dominated by aspen, and optimal for rockfall protection.
- Wild ungulates found suitable habitats in the avalanche track and in the control.
- Maintaining avalanche-disturbed areas in the landscape can benefit biodiversity and wildlife habitat.

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Supplementary Material S1 Species list and abundance scores (Braun-Blanquet, 1932) for the regeneration, shrub, and herbaceous layers of the control site, the old disturbance, and the more recently disturbed site.

Map KML file containing the Google map of the most important areas described in this article.

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Effect of avalanche frequency on forest ecosystem services in a spruce–fir mountain forest

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ABSTRACT

Mountain forests provide important ecosystem services, such as protection against natural hazards, carbon sequestration, and plant and animal biodiversity. Natural disturbances occurring in forests can alter the provision of ecosystem services to local and offsite communities, but their influence on multiple service tradeoffs has rarely been analyzed.

Our aim is to analyze the effect of avalanche frequency on the provision of ecosystem services in a mountain forest in the Italian Alps. We sampled tree and understory vegetation, soil carbon, and intensity of the browsing damage at 10 plots at each of the following observation sites: (1) an active avalanche track ("recent disturbance"), (2) an area last disturbed in 1959 by avalanches ("old disturbance"), occupied now by a dense aspen forest, and (3) the regularly managed spruce–fir stand ("control"). We computed metrics of plant diversity (Shannon and evenness indices), aboveground and belowground carbon stocks, and a browsing index on regeneration and shrubs as a proxy for ungulate habitat. Finally, we assessed the ability of forests in each site to mitigate rockfall hazard.

In our study, higher avalanche frequency was associated with lower carbon stock, higher species diversity, and lower protection against rockfall. Of all species found in the avalanche track, 54% were exclusive to that site. After 50 years, the post-disturbance stand provided a very high protection effect against rockfall, but was temporarily unsuitable for wild ungulate habitat, due to the high tree density and lack of open areas. Species richness and diversity were lower in older than in more recently disturbed sites, and not significantly different than the control stand. The control stand fulfilled the requirements for minimal protection against rockfall, but may lose its effectiveness in the near future due to senescence or disturbance-related mortality of canopy trees.

Elucidating the tradeoffs between ecosystem services and disturbance frequency will support managers in planning management actions (e.g., avalanche protection measures), and assess tradeoffs between the need to mitigate risks in the most vulnerable areas and the opportunity to improve the provision of ecosystem services where some disturbance can be allowed to occur.

1. Introduction

Mountain forests throughout the world provide a variety of important ecosystem services, including protection against natural hazards (e.g., floods, avalanches, and landslides), carbon sequestration, provision of natural resources (e.g., dairy products, timber as renewable raw material for energy production and for construction), tourism and recreation, fresh water regulation, and plant and animal biodiversity (Grêt-Regamey et al., 2008a). Even where production or supply services are not the main interest, e.g., in those parts of the Alps where timber extraction has ceased to be profitable due to socio-economic changes (Conti and Fagarazzi, 2004; Walther, 1986), regulatory functions play an important role for both local and offsite communities.

In particular, Alpine regions have developed programs to identify and manage direct protection forests, i.e., forests that protect human settlements or infrastructures from gravitational hazards such as rockfall, avalanches, and debris flow (Berger and Rey, 2004; Brang, 2001; Brang et al., 2006; Wehrli et al., 2007). The effectiveness of forest stands, or of specific stand structures, in mitigating natural hazards has been assessed by field surveys, experiments, and empirical or physical models (Bigot et al., 2008; Dorren et al., 2004; Motta and Haudemand, 2000; Teich et al., 2013). Such research has provided land administrators with quantitative tools to assess risk and management priorities in time and space (Frehner et al., 2005; Grêt-Regamey et al., 2008b;

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Olschewski et al., 2012; Teich and Bebi, 2009), and has enabled science-based allocation of resources to maintain, promote, or rehabilitate the forest protective function.

From the biodiversity point of view, the Alps exhibit a complex geomorphology and an array of microclimates which contribute to a wide variety of habitats (i.e., 100 of 198 habitat types listed in Annex I of the Habitats Directive 92/43/EEC), and high levels of biodiversity. The alpine biogeographic region of Europe hosts about 7000 plant species (Ozenda and Borel, 1994), that is more than a third of the flora recorded in Europe west of the Urals, and almost 400 endemic plants (Aeschimann et al., 2004). The fauna of the Alps might reach 30,000 species (Chemini and Rizzoli, 2003). A total of 165 species and subspecies are highly protected (Annex II of the Habitats Directive 92/43/EEC), while the region includes important refugia for plants and especially for animals with large home range requirements (Condé et al., 2006). In the 20th century, the abandonment of mountain fields, meadows and grazing lands, and the expansion of shrubs and forests with an accompanying reduction of clearings, as well as the intensification of tourism and human presence, have greatly affected suitable habitats for plant and animal species, determining an increase of forest-related taxa and a demise of grassland species (Falcucci et al., 2006; Laiolo et al., 2004; Niedrist et al., 2008; Pellissier et al., 2013).

Finally, many temperate mountain forests are currently a carbon sink (Ciais et al., 2008; Goodale et al., 2002), due to their predominantly young age, the naturally occurring afforestation of fallow lands, and the ongoing environmental changes, i.e., climate warming and nitrogen (N) deposition (Bellassen et al., 2011). However, adapting forest management to maximize carbon stocking is subject to many uncertainties, such as the quantity and processes of carbon in the forest soil (Lal, 2005), or the effect of natural disturbances (Gimmi et al., 2008; Liu et al., 2011).

Disturbances are ubiquitous in forest ecosystems (Franklin et al., 2002). In forests of the European Alps, large, stand-replacing disturbances are relatively rare due to the high degree of landscape fragmentation and to the pervasive control by man, e.g., by active fire and avalanche suppression (Brotons et al., 2013; Kulakowski et al., 2006) or insect outbreak monitoring and control (Faccoli and Stergulc, 2004). However, disturbances still occur at spatio-temporal scales relevant to the provision of ecosystem services to local communities, e.g., on occasions of extreme fire seasons (Veraverbeke et al., 2010), regional drought spells inducing forest decline events (Rigling et al., 2013), or extra-tropical cyclones (Ulbrich et al., 2001). Recent research has been addressing the questions related to: a) the quantification of ecosystem services (Haines-Young et al., 2012; Millennium Ecosystem Assessment, 2005), b) the resolution of conflicts between non-compatible ecosystem services (Briner et al., 2013; Bullock et al., 2011; Grêt-Regamey et al., 2013; Nelson et al., 2009), and c) the impact of climate change on the provided services (Elkin et al., 2013; Lindner et al., 2010; Metzger et al., 2006). However, the influence of natural disturbances on multiple service tradeoffs has rarely been analyzed (e.g., Spencer and Harvey, 2012), especially in forest ecosystems.

Avalanches are one of the dominant disturbance agents in the Alps (Bebi et al., 2009). High-frequency avalanches shape the ecosystem in which they occur, and exert a strong selective pressure on plant and animal species living in the avalanche track and runout zone (Butler, 1985; Rixen et al., 2007). On the other hand, low-frequency, high-intensity events have the potential to reset the ecological succession, by replacing mid-seral species by early-seral colonizers capable of taking advantage of the new environmental conditions in the avalanche aftermath (Erschbamer, 1989). In both cases, avalanches can greatly affect the provision of ecosystem services and the functioning of forest ecosystems, not only in the area directly perturbed (Viglietti et al., 2010), but also at landscape scale, e.g., by modifying connectivity and the spatial pattern of the forest matrix (Butler, 2001). However, their role in relation to the provision of ecosystem services is still unexplored.

The aim of this paper is to analyze the effect of avalanche frequency on the provision of ecosystem services in a mountain forest. We quantified carbon stocking, wild ungulate habitat, plant diversity, and rockfall protection and compared all of them across three contiguous sites of (1) a yearly disturbed area, (2) a 50-year old disturbance, and (3) a regularly managed forest not disturbed by avalanches ("control"). Finally, we modeled the effect of disturbance frequency and other environmental predictors (i.e., stand structure, species composition, and soil cover classes) on the current level of forest ecosystem service provision, in order to assess which agent was responsible for the largest effects on the chosen services.

1.1. Area description

Our study area (Fig. 1) is the Cranmont avalanche path, in the municipality of Pré Saint-Didier (Aosta, Italy: 45°45′54″ N, 6°59′12″ E). The avalanche track runs in the gully of the Cranmont creek from 2680 to 1030 m a.s.l. on a northeast-facing slope. The mean slope angle of the release zone is 35°. Mean annual temperature and precipitation at the runout zone are 6.9 °C and 1072 mm, respectively (interpolation of observed data for the years 1950–2000) (Hijmans et al., 2005). Below the timberline (at 2000–2250 m a.s.l.), forests are dominated by European larch (*Larix decidua* Mill.) in the subalpine belt (Habitat 9420 of the Directive 91/244/CEE) and Norway spruce (*Picea abies* (L.) Karst.) in the montane belt (Habitat 9410), with sporadic Scots pine (*Pinus sylvestris* L.) on rock ridges, silver fir (*Abies alba* Mill.) at locally moister sites, and broadleaves such as aspen (*Populus tremula* L.), birch (*Betula pendula* L.), and willow (*Salix caprea* L.). According to a recent regional forest inventory (Camerano et al., 2007), stand density, quadratic mean diameter, and dominant height in the area are in the range of 160–680 trees ha^{-1}, 23–35 cm, and 15–26 m, respectively.

No specific information on past forest management in the study area was available. However, looking at field evidence (stumps), low deadwood amount, and at the reverse-J shape of the diameter distribution (see below), we can assume that this stand was (and still is) treated according to consuetudinary management practices in mixed montane Norway Spruce forests of the Alps, i.e., after recovery from extended clearcuts during Word War II, maintaining an uneven-aged structure by single tree or small group selection every 10–20 years, and promoting groups of naturally established regeneration (Motta et al., 2000, 2010, 2015).

The Regional Avalanche Cadastre (CRV) (Lunardi et al., 2009) reports that an avalanche occurred 72 times between 1913 and 2011, usually in January or February (35 occurrences), and was characterized by a variable behavior and severity. The avalanche type has been either loose snow or slab (width of starting zone: a few to 300 m). The avalanche has repeatedly damaged human infrastructure in the runout zone (two records of housing damage, eight records of road damage). Information from the local people implied that the avalanche usually occurs, not necessarily to its largest potential extent, many times a year (up to ten times depending on the snow conditions). In a winter season, the first events often run straight down to the Dora Baltea river, while the latter ones, influenced by the previous deposits, tend to be deflected towards the north (Fig. 1). In cases of large events in the advanced snow season, the avalanche can more easily have a larger width and overcome its yearly track to the South, influencing the older forest. Damage to the forest outside the common avalanche track has been recorded on December 24th, 2009, and December 29th, 1959 (Fig. 2a). The latter event had an extraordinary severity, destroying trees in the previously undisturbed forest, and accumulating a deposition height of 20 m in the runout area. From the analysis of historical photographs (Fig. 2a) it is evident how the damage to the older forest was produced from the powder component of the avalanche flow; this area is currently occupied by a dense aspen forest (Fig. 2b). At the transition between the track and deposition zones, we identified three different study sites

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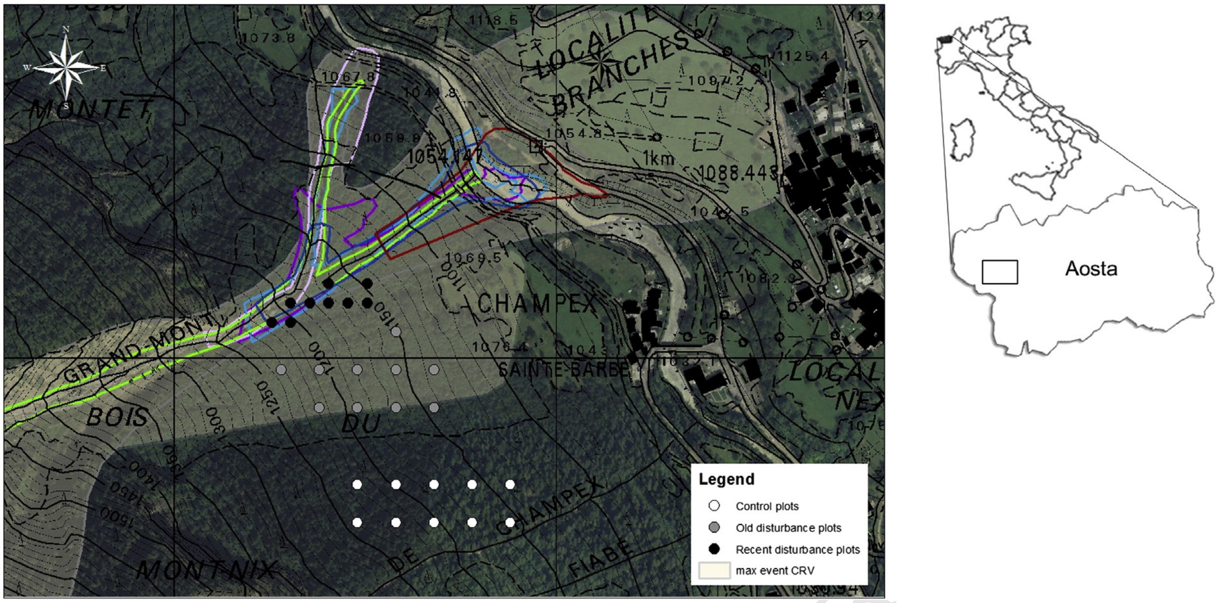

Fig. 1. Study area location, maximum avalanche perimeter from the regional avalanche cadaster (CRV) and sampling design. Colored perimeters represent several occurrences of the avalanche as recorded by CRV. White dots: recent avalanche site; gray dots: old avalanche site; black dots: control site.

according to the frequency of disturbance (Fig. 1, Fig. 2b), which are described in the next section.

Finally, the whole study area is mapped as a direct protection forest (Meloni et al., 2006), i.e., one that protects downslope human settlements and infrastructures from gravitational hazards. Here, the hazard is represented by rockfall potentially released from within-forest cliffs at elevations of about 1500–1700 m a.s.l. The bedrock in Cranmont is made of metamorphic units belonging to the North-Pennidic domain of the Alps (Sion-Courmayeur Zone), with alternating calcite marble and micaceous–chloritic carbonate schists (Perello et al., 1999). The width of the rockfall-source area is about 300 m, but there is considerable potential for lateral rockfall spread due to the fan-shaped topography of the slope. Individual rocks witnessed in the field ranged from 10 to 100 cm in average diameter.

2. Material and methods

2.1. Sampling design

We established a chronosequence of increasing disturbance frequency, and decreasing time since the last disturbance, by comparing the following sites: 1) recent disturbance (R) by using the track width of the majority of the avalanches recorded in the Cadastre (i.e., avalanche return period of one to a few years); 2) old disturbance (O), by reconstructing the perimeter of the 1959 event from pre-disturbance historical aerial imagery (1954) and oblique photographs of the event (i.e., avalanche return period of more than 50 years), and 3) the control (C) forest (regular forest management, no avalanches). In order to control for undesired topographic and climatic variability, we constrained sampling between elevations of 1125 and 1300 m a.s.l., corresponding to the top and bottom boundary of forest management unit 38 (source: municipal Forest Management Plan). Within each site, we randomly established 10 sampling plots, ensuring a minimum distance of 20 m from the site edge, and of 25 m between plots. The maximum distance between any two plots was 280 m (Fig. 1).

Sampling was carried out in summer 2012. In each plot we sampled the following: (1) diameter at breast height (DBH), height (H) and species of all living trees (DBH > 2.5 cm) within a 12 m radius from the plot center; (2) percent cover by the tree, shrub, herbaceous layers, and exposed mineral soil, within a 5 m radius from the plot center; (3) species and frequency of all regeneration individuals (H > 10 cm, DBH < 2.5 cm) in the 5 m plot; (4) species and visually estimated cover of each vascular plant in the 5 m plot (floristic nomenclature according to Aeschimann et al., 2004); (5) severity of browsing damage (0: none, 6: 100% browsing or dead individual) (Motta, 1996) to all regeneration individuals and shrubs within each 5 m plot. Finally, we estimated tree age based on increment cores extracted at 50 cm height from one randomly selected tree in each of the small (DBH < 15 cm), medium (15 < DBH < 25 cm), and large (DBH > 25 cm) tree size classes per 12 m plot.

For the analysis of carbon stocks, we sampled the following: (6) height and average crown radius (CR) of all shrubs with CR > 100 cm; (7) diameter and decay class (1: sound, 3: soft) of all coarse woody debris (CWD) elements (diameter > 10 cm) along two perpendicular linear transects (length = 24 m per transect) concentric to the plot center; (8) herbs and litter in three 40 × 40 cm subplots, at the plot center and at a 2 m distance in a northward and southward direction; (9) mineral soil at 0–5 cm depth, sampled at each subplot by using a 5 cm × 25 cm^2 metal cylinder. Herbs, litter, and soil samples were subsequently pooled, oven dried (105 °C for 72 h) and weighted in the lab to obtain their biomass; soil samples were preliminarily sieved at 0.5 mm.

2.2. Data analysis

For each sampling plot, we computed total tree density, basal area, species composition by density and basal area, quadratic mean diameter (QMD), mean height, and total tree volume (V) by applying DBH-to-volume equations for spruce (Nosenzo, 2005) and broadleaves (Castellani et al., 1984). Following preparation of tree cores (Stokes and Smiley, 1996), we computed the total tree age at coring height from each core by summing the tree ring count and an estimate of missing rings near the pith obtained by means of a pith locator. Using the sample of measured ages, we fitted a linear Age-DBH model for each, and used it to compute missing ages for all tallied trees.

The volume and dry biomass of coarse woody debris (W_{CWD}) were obtained by applying the equations for line intercept sampling (Pearson et al., 2007) (Eq. 1):

$$W_{CWD} = -\frac{1}{8}\pi L\sum\left(d_{CWD}^2 k\right), \tag{1}$$

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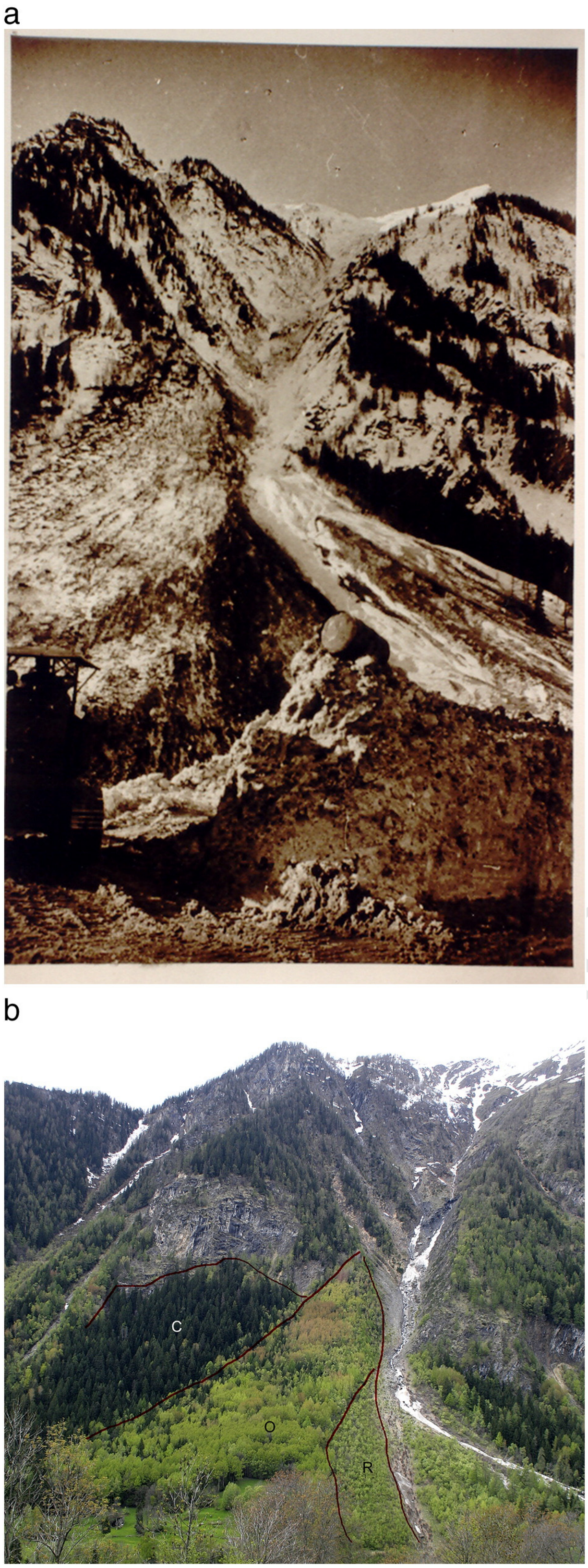

Fig. 2. The avalanche event in 1959 (a) and 2009 (b), with indication of the control (C), old (O), and recent (R) avalanche sites.
Image (a) by Ufficio Neve e Valanghe — Regione Autonoma Valle d'Aosta, (b) by the authors.

where L is transect length, d_{CWD} is the measured diameter of each coarse woody debris element, and k is the wood density associated with each decay class (class 1: 0.43 t m^{-3}, class 2: 0.34 t m^{-3}, class 3: 0.19 t m^{-3}) (Pearson et al., 2007). The dry biomass of living trees (W_T) was obtained by applying a biomass expansion equation to the total standing volume of each plot (Penman et al., 2003) (Eq. (2)):

$$W_T = (1+R)(V \cdot BEF \cdot k_T), \tag{2}$$

where BEF is biomass expansion factor, R is the belowground: aboveground biomass ratio, and k_T is species-specific wood density (Table 1). Shrub biomass (W_S) was computed allometrically (Ohmann et al., 1976) (Eq. (3)):

$$W_S = ax^b, \tag{3}$$

where x is shrub height for hazel (*Corylus avellana* L.) and crown area (CR^2) for all other species, and a and b are species-specific allometric coefficients (Table 2). Carbon in the coarse woody debris, trees, shrubs, herbs, and litter fractions were computed on a per-hectare basis by assuming a carbon content of 50% in the dry biomass. Soil carbon content ($C_{\%}$) was determined in the lab by dry combustion using a Carlo Erba elemental analyzer, and subsequently converted to carbon biomass on a per-hectare basis (C_{soil}) (Eq. (4)):

$$C_{soil} = C_{\%} \cdot \text{BD} \cdot \text{depth}, \tag{4}$$

where BD is dry bulk density of the soil, and depth is the sampled soil depth (5 cm).

Plant diversity was assessed at the plot level by computing total species richness (SR), Shannon diversity index (H′, Eq. (5)) and Shannon equitability index (E, Eq. (6)) (Magurran, 1988):

$$H' = -\sum p_i \ln p_i, \tag{5}$$

$$E = \frac{H'}{\ln SR}, \tag{6}$$

where p_i is the relative abundance of species i in the plot. Species marked as sporadic were assigned an abundance of 0.3 (Reichelt and Wilmanns, 1973).

Ungulate habitat (red deer *Cervus elaphus* and roe deer *Capreolus capreolus*) was assessed by three different indices, taking into account seasonal food availability and hiding cover requirements (Black et al., 1976). Summer food availability was quantified using the sum of herbaceous and shrub cover as a proxy (Moser et al., 2008). Winter food availability, critically important to both red and roe deer, was assessed by computing a browsing index (IB) on shrubs and regeneration for each plot (Boulanger et al., 2009) (Eq. (7)):

$$\text{IB} = \sum \frac{p_i dam_i}{p_i pal_i}, \tag{7}$$

where dam_i and pal_i are the average browsing damage and palatability (Table 3) of species i, respectively. Browsing intensity has been used in the past to assess habitat use by wild ungulates (Moser et al., 2008), and can be indicative of winter use if computed on resources normally grazed during such season, i.e., in the absence of herb cover. Finally, deer hiding cover (HC) was estimated as a function of the sum of tree DBH in a stand (Eq. (8)), using a trigonometric algorithm previously

Table 1
Parameters for the calculation of stand biomass.
From Vitullo et al. (2007).

Cover type	Biomass expansion factor	Dry:fresh weight	Root:shoot ratio
Conifers	1.29	0.38	0.29
Broadleaves	1.47	0.53	0.24
Shrubs	1.44	0.52	0.42

Table 2
Parameters of the allometric equations for shrub biomass.
From Ohmann et al. (1976).

Species	x	Parameter	Twig biomass	Stem biomass	Total biomass
Corylus avellana	Stem height	a	0.003268	0.00002089	0.0002791
		b	1.373	2.98	2.52
Lonicera spp.	Crown area	a	0.0819	0.7513	–
		b	0.6072	0.625	–
Other shrubs	Crown area	a	0.3504	0.8201	–
		b	0.2888	0.577	–

developed for lodgepole pine (*Pinus contorta* Douglas) (Smith and Long, 1987). The algorithm assumes uniform tree spacing and crown height higher than 1 m (i.e., tree crowns do not contribute to hiding), and assumes that hiding cover is adequate when an average of 90% of an adult elk is hidden at a distance of 60 m.

$$HC = 100 - 115.8(0.61)^{0.0003937\sum dbh} \tag{8}$$

Finally, we assessed rockfall protection by using the online tool RockforNET, that computes the percentage of rocks that surpasses the forested area (Probable Residual Rockfall Hazard, PRH) given rock size, topography, and stand structural characteristics (Berger and Dorren, 2007). Parameters entered in RockforNET were: rock density = 2700 km m^{-3}, rock shape = rectangle, rock dimensions = (a) 50 × 50 × 20 cm (moderate size) and (b) 100 × 100 × 40 cm (large), height of cliff = 50 m, mean gradient of the slope = 35°, length of unforested slope = 20 m. The length of forested slope was set at a constant value of 250 m in order to make meaningful comparisons between stands regardless of their actual position on the slope (Cordonnier et al., 2013). Stand density, basal area (DBH > 8 cm), and tree species composition were entered on a per-plot basis.

Carbon stock, ungulate habitat metrics, plant diversity metrics and PRH were compared across sites by means of non-parametric Kruskal–Wallis test with pairwise post-hoc Tukey comparison ($p < 0.05$).

3. Results

3.1. Forest and vegetation structure

The avalanche radically changed the forest composition and structure (Table 4) in both the avalanche recent disturbance and the old disturbance. The main impacts of increasing avalanche frequency were: lower tree age and size, higher share of deciduous species in both adult and juvenile layers, higher shrub and herb cover, and a bell-shaped response of tree density and cover (i.e., higher for intermediate time since disturbance) (Fig. 3). Between-plot variability was generally higher in the old disturbance and control sites, while the recent disturbance site exhibited pretty homogenous conditions, except for herb, shrub, and bare soil cover.

Table 3
Species palatability scores, mean browsing damage (0: none, 6: 100% browsed), and average per hectare frequency of regeneration and shrubs in the three observation sites. Only species where 10 or more individuals were samples are included.

Species	Palatability	Mean browsing damage	Average per hectare frequency		
			Control	Old disturbance	Recent disturbance
Abies alba	0.8	4.7	799	561	1249
Acer spp.	0.9	1.4	311	130	26,141
Berberis vulgaris	0.05	1.1	76	229	3333
Betula pendula	0.3	0.5	1469	4047	66,643
Corylus avellana	0.7	2.5	446	803	66,667
Fraxinus excelsior	0.9	0.9	183	630	90,848
Lonicera spp.	0.6	2.0	1516	3210	206,667
Picea abies	0.3	0.4	708	399	4444
Populus tremula	0.4	1.7	0	58	6780
Salix spp.	0.6	1.5	247	333	154,544
Sorbus spp.	0.6	1.1	725	185	730
Rosa spp.	0.1	2.2	25	13	2222
Rubus spp.	0.6	1.1	13	64	148,889

In the control area the forest was dominated by Norway spruce (53% basal area on average), silver fir (20%), and larch (10%), with sporadic broadleaves (0–20%). The trees were quite dense (1760 per hectare on average, DBH > 2.5 cm), with a mean diameter around 21 cm and a typical uneven-aged size distribution (Fig. 4). Maximum tree age in the dendrochronological subsample trees ranged from 71 years (aspen) to 210 years (spruce); after fitting DBH-age models (Fig. 5), we estimated that the oldest trees in the control area could be around 230 years old. The canopy had a variable tree cover of 20–80%, with treefall gaps allowing the accumulation of coarse woody debris on the ground, and the establishment of dense patches of regeneration of spruce and broadleaves alike. Herb and shrub cover was scarce (5% and 13% on average, respectively).

In the old disturbance site the forest was dominated by a dense layer of pole-stage aspen (4000 trees per hectare on average, QMD = 13 cm) (Table 4). The canopy was closed. Spruce was less abundant both in the canopy (37% of basal area on average) and in the regeneration layer, except for some older spruce trees (>100 years) that were probably left as living legacies from before the last disturbance event. Mean tree age (from both measured and modeled ages) was 45 years; some spruce trees older than 50 years were found, probably as legacies of the pre-disturbance stand (i.e., trees that were tilted but not broken by the avalanche), but none was older than 130 years (Fig. 6).

Finally, in the avalanche track, the high frequency of disturbances resulted in a young stand dominated by young, sprouting broadleaves (98% of basal area on average, QMD = 6 cm). All trees were younger than 50 years (mean tree age: 24 years), and most stems were shorter than 8 m in height. Tree density, volume, basal area, and tree cover were all very low (Table 4). Regeneration was dominated by deciduous species, reaching up to 375,000 per hectare when individual sprouts on each stump were counted.

3.2. Ecosystem service assessment

The average amount of carbon in the aboveground, belowground, coarse woody debris, litter, and soil compartments was inversely proportional to the disturbance frequency, i.e., higher in the control and lower in the avalanche track (Fig. 7). The latter had more carbon in the herb and shrub layers, but the total amount was significantly higher in the control stand (400 Mg ha^{-1} on average) (Table 5). Soil carbon usually accounted for about 50% of the total. C/N ratio varied in the range of 18–26 in the control, 17–25 in the old disturbance, and 17–22 in the recent disturbance site.

Species richness of the regeneration, shrub and herbaceous layers in the control, old avalanche, and recent avalanche was 44, 43, and 77 species, respectively (Supplementary Material S1). Out of 98 species found, 27 were common to all sites, while 42 were exclusive of the avalanche track (i.e., 54% of all species found in that site). Six species were exclusive of the old disturbance, and only eleven of the control. Consequently, the avalanche track showed the highest plant diversity (Shannon index), although evenness was lower than in the other two sites, due to the dominance of a few shrubs (hazel: 32% average cover, *Salix purpurea*: 6%, *Lonicera nigra*: 6%), and graminoid species (especially *Trisetum flavescens*, 9%). The old disturbance and control did not differ significantly in their diversity indices (Table 5).

Winter resource use by ungulates (i.e., intensity of browsing on regeneration and shrubs) was highest in the control plots and lowest in the old disturbance ($p < 0.05$), even if with a very large variability throughout the study area (0 to 90%). Silver fir was the most damaged species, followed by hazel, *Lonicera* (among shrubs), aspen, *Salix*, and

Table 4
Summary of stand structural variables in the control, old, and recent avalanche sites.

Variable	Units	Control		Old disturbance		Recent disturbance	
		Mean	SE	Mean	SE	Mean	SE
Basal area	$m^2\ ha^{-1}$	56.1	12.02	46.9	5.61	6.5	1.70
Tree density	ha^{-1}	1763	270.9	3961	658.3	2065	406.4
QMD	cm	20.8	2.17	12.8	0.59	6.0	0.40
Mean height	m	13.7	0.72	10.4	0.31	4.6	0.37
Tree volume	$m^3\ ha^{-1}$	527.3	48.81	372.0	33.53	20.5	7.03
CWD volume	$m^3\ ha^{-1}$	35.6	17.25	21.4	5.84	6.6	2.89
Mean age	years	64	3.7	45	2.6	24	2.4
Basal area by spruce	%	53	7.4	37	5.9	1	0.9
Basal area by fir	%	27	9.5	6	2.0	1	0.1
Basal area by larch	%	5	3.5	3	2.6	1	0.6
Basal area by broadleaves	%	9	2.5	54	6.9	98	1.2
Tree cover	%	57	5.8	69	4.5	12	3.7
Shrub cover	%	13	2.5	15	4.7	53	8.2
Herb cover	%	5	1.0	4	1.1	48	7.6
Bare soil	%	3	0.8	3	1.3	3	1.1
Regeneration[a] density	ha^{-1}	10,309	4232.5	4039	2422.0	8342	3590.0
Regeneration[a] by spruce	%	18	6.5	8	4.3	1	1.1
Regeneration[a] by broadleaves	%	53	11.8	75	10.0	98	1.4

[a] Regeneration: H > 10 cm, DBH < 2.5 cm.

Acer (among tree species) (Table 3). Summer resource availability (herb and shrub cover) and hiding cover by trees were respectively higher and lower in the recent disturbance site (Table 5).

The most effective stand for rockfall protection was the old disturbance site. Currently, PRH against moderate-sized rocks reaches 95% in both the old disturbance and the control sites, and decreases to 83 and 74% respectively on large-sized rocks. In the avalanche track the protection effect is negligible (mean PRH: 11% against moderate sized rocks, and 4% against large rocks), due to insufficient tree density and large treeless areas (Table 5).

4. Discussion

Following stand-replacing disturbance, the dominant spruce–fir canopy (Fig. 8c) is replaced by early-seral broadleaves (Fig. 8a), eventually dominated by aspen that forms a dense pole-stage forest 50 years after the event (Fig. 8b). Spruce and fir regeneration can then establish below the aspen layer, taking advantage of its higher shade tolerance, of seeds dispersed by trees surviving the avalanche, and of disturbance legacies such as coarse woody debris and pit-mound topography (Bottero et al., 2013).

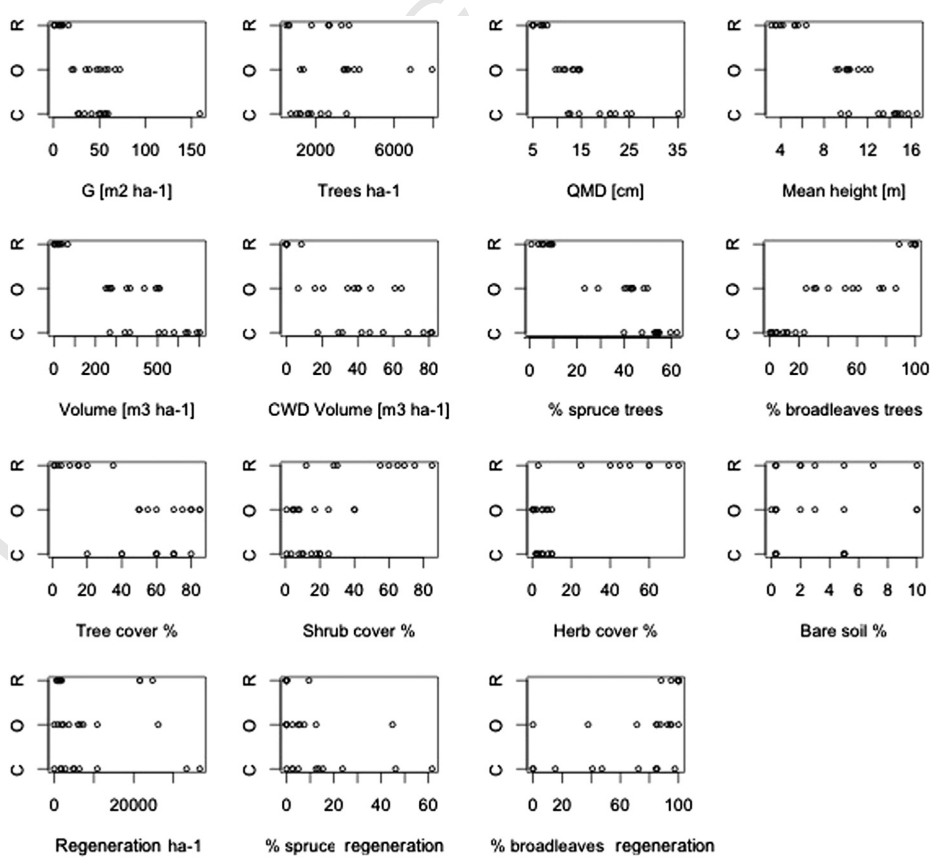

Fig. 3. Observed stand structure parameters in plots from the control (C), old (O), and recent (R) avalanche sites.

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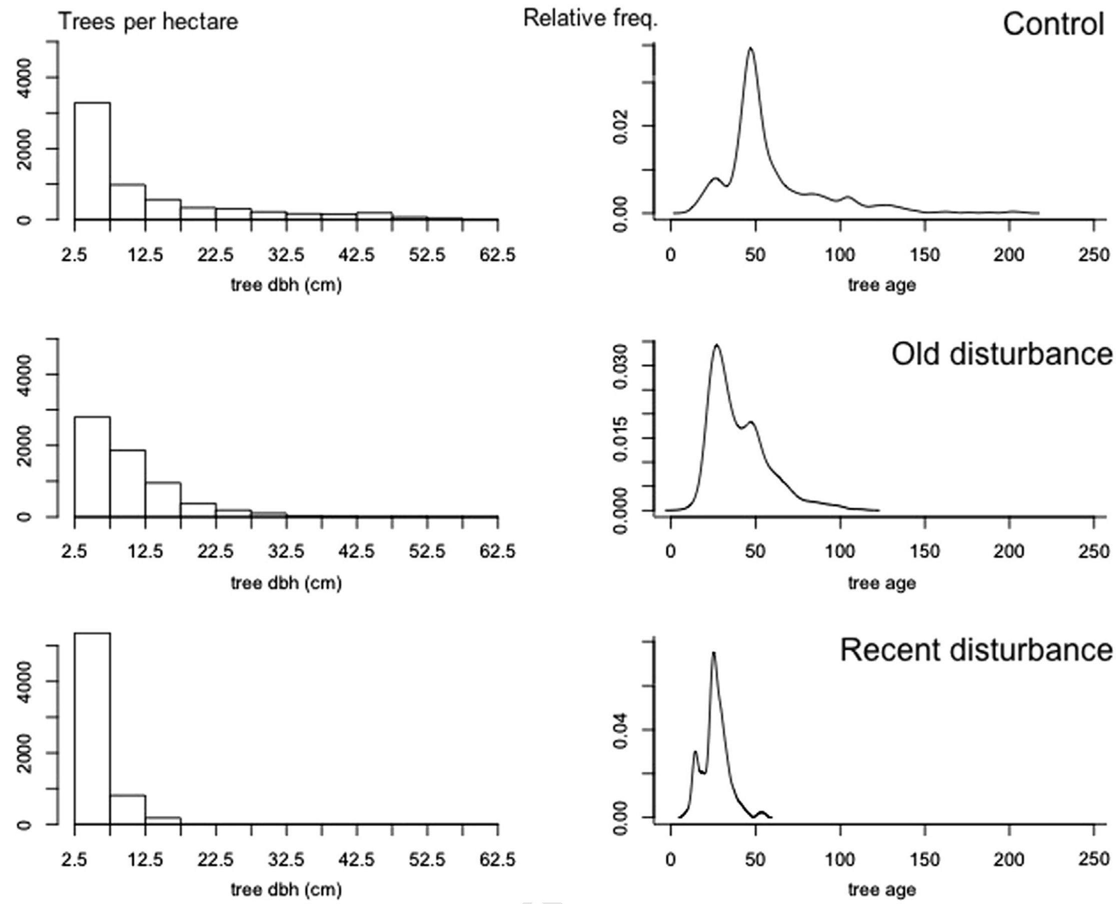

Fig. 4. DBH (frequency distribution) and age (smoothed relative frequency distribution) in the control, old, and recent avalanche sites.

In the study area, higher avalanche frequency was associated with: (1) lower aboveground and belowground carbon stock, (2) higher species richness (but no change in diversity), (3) higher summer resource availability, intermediate winter resource use and lower hiding cover for wild ungulates, and (4) lower protection against multiple-sized rockfall. After 50 years, high stem density of post-disturbance stands was optimal for protection against rockfall and ungulate hiding requirements, but at the same time resulted in poor resource availability for wild ungulates due to the scarce herb and regeneration cover. Species richness and diversity in the old disturbance site were not significantly

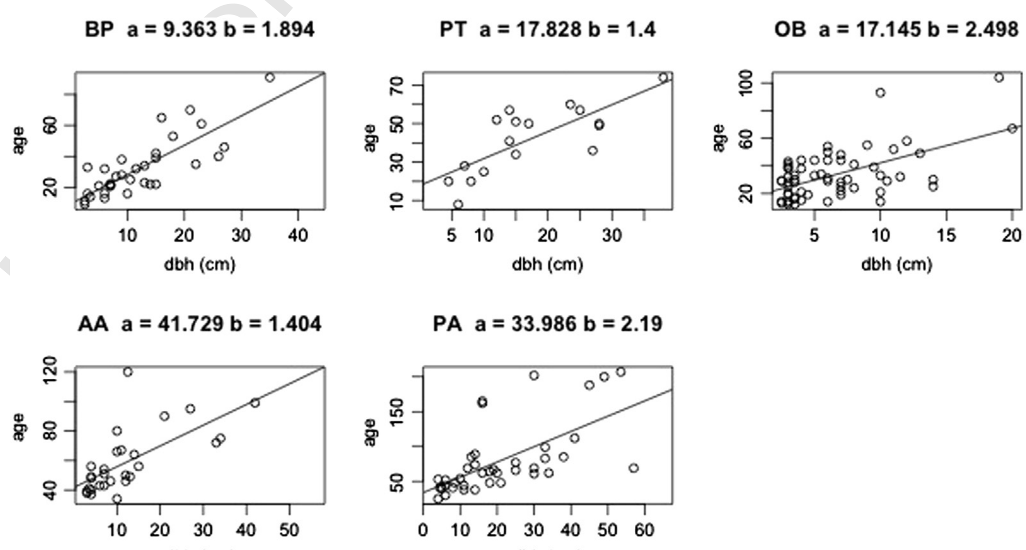

Fig. 5. Individual tree DBH-age models for spruce (PA), silver fir (AA), birch (BP), aspen (PT) and other broadleaves (OB) in the study area (dendrochronological subsample, all treatments pooled). Model form was age = a + b DBH.

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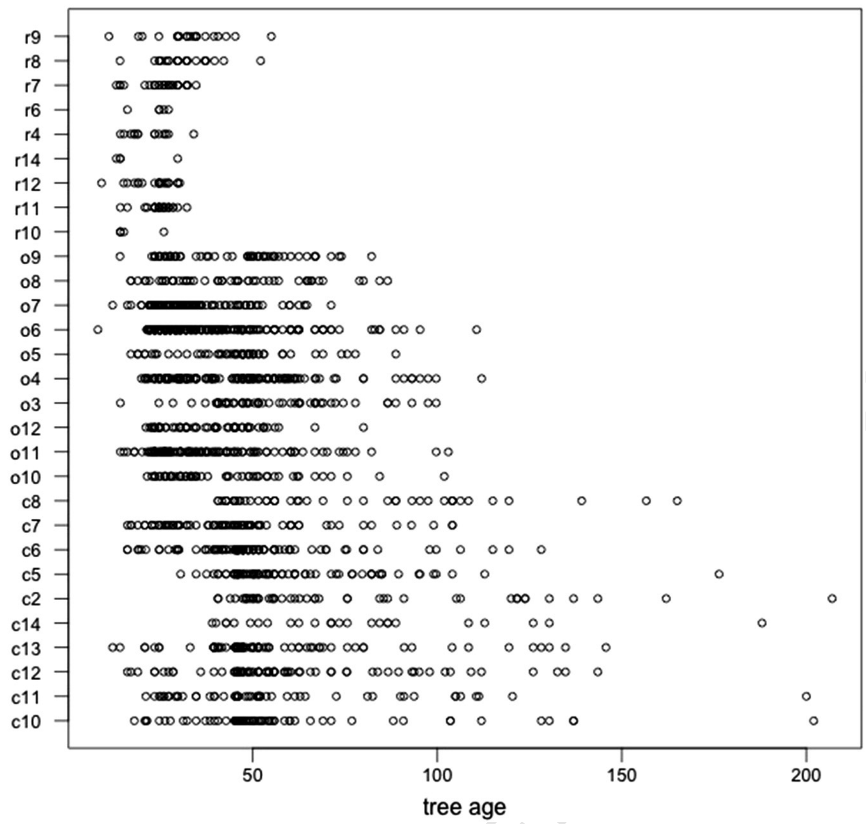

Fig. 6. Scatterplot of tree ages (all species – both measured and modeled tree age) in all sampling plots from the control (C), old (O) and recent (R) avalanche sites.

different than the control, where the forest was managed according to common single tree selection silvicultural practices.

4.1. Carbon stock

Carbon stocks followed a predictable gradient of post-disturbance recovery and buildup. Many studies of carbon stocks in post-disturbance chronosequences have highlighted a carbon source/sink dynamics for stand-replacing disturbance, involving a rapid pulse emission followed by net uptake that gradually declines with the aging of the canopy (Bond-Lamberty et al., 2004; Gough et al., 2007; Pregitzer and Euskirchen, 2004; Richter et al., 1999; Thornton et al., 2002). In our study area, the regularly managed forest stocked about 400 Mg C ha^{-1} on average. Values for aboveground carbon stocks were consistent with those found in undisturbed spruce forests of the Alps (e.g., 207 Mg C ha^{-1} in living trees at 130 years of age, Thuille et al., 2000). Soil stocks (>200 Mg C ha^{-1} on average) were higher than some values found in literature for comparable ecosystems (e.g., 81 to 188 Mg C ha^{-1} in the organic and mineral layers on acidic soils in Austria: Berger et al., 2002; Pötzelsberger and Hasenauer, 2015) but consistent with uneven-aged spruce forests of similar age in boreal ecosystems (e.g., 199 Mg ha^{-1}: Nilsen and Strand, 2013). Unless significantly disturbed by stochastic agents (e.g., wind damage, bark beetles, exceptional avalanches), the spruce forest has the ability to function as a sink well into its maturity stage, as shown by recent research on managed and old-growth forest (Gleixner et al., 2009; Krug et al., 2012; Luyssaert et al., 2008; Zhou

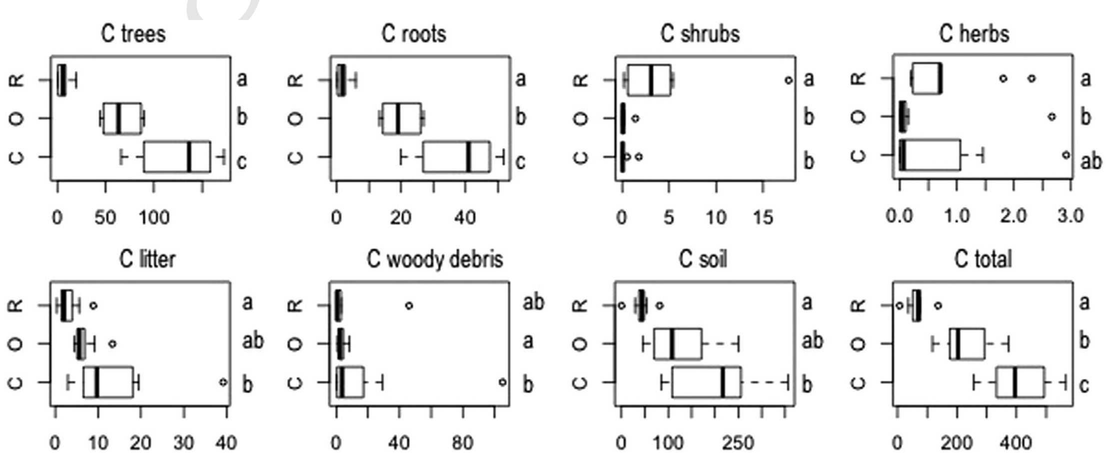

Fig. 7. Carbon stocks [Mg ha^{-1}] by ecosystem component in the control (C), old (O), and recent (R) avalanche sites. Sites marked by similar letters did not differ significantly (Kruskal–Wallis test, $p > 0.05$).

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Table 5
Summary of ecosystem service values in the control, old, and recent avalanche sites. Sites marked by similar letters did not differ significantly (Kruskal–Wallis test, $p > 0.05$).

		Control		Old disturbance		Recent disturbance	
Variable	Units	Mean	SE	Mean	SE	Mean	SE
Herb + shrub cover (summer resource)	%	11 a	1.6	10 a	3.1	58 b	6.5
Browsing index (winter resource)	%	38 a	5.4	21 b	5.4	26 ab	4.7
Elk hiding cover	%	95 a	0.9	99 a	0.1	29 b	12.2
Total C	Mg ha^{-1}	402 a	30.1	222 b	26.2	64 c	11.8
Shannon index	–	1.5 a	0.12	1.6 a	0.12	2.1 a	0.41
Evenness	–	0.7 a	0.04	0.8 a	0.05	0.7 a	0.12
PRH (moderate size rocks)	%	95 a	5.2	99 a	2.3	11 b	6.7
PRH (large size rocks)	%	74 a	6.4	83 b	3.3	5 c	2.1

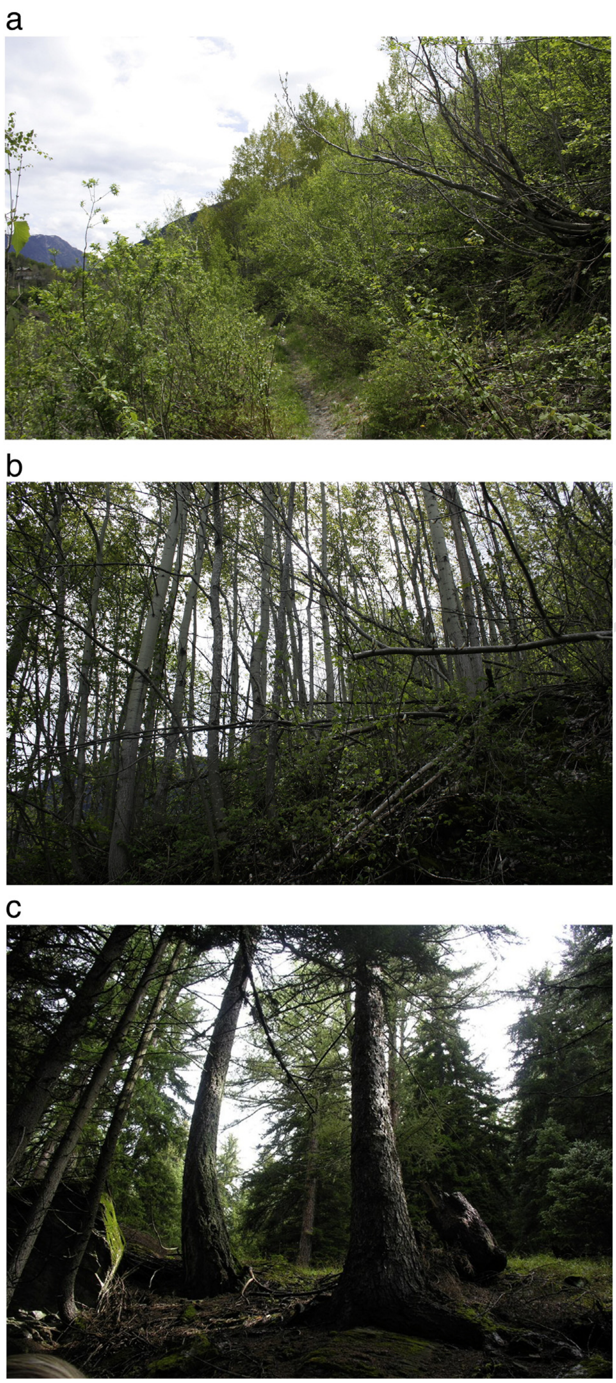

Fig. 8. Photographs taken during field sampling in the control (a), old (b), and recent (c) avalanche sites.
Images by the authors.

et al., 2006). The effect of different types of forest management on soil and total C sink, however, is still uncertain, but greatly depends on the intensity and frequency of tree removals (e.g., Jandl et al., 2007; Nave et al., 2010; Nilsen and Strand, 2013). The fact that soil is stocking more than 50% of overall ecosystem C is well acknowledged by the literature (Lal, 2005) but rarely measured in the field and often overlooked when computing sequestration/emission balances in forest ecosystems. The belowground:aboveground C ratio did not differ between the old disturbance site and the regularly managed forest, suggesting the absence of significant species-specific differences in root turnover and carbon mineralization rate.

The 50-year old aspen forest is stocking about 200 Mg C ha^{-1} on average, corresponding to a mean uptake of about 3 Mg C ha^{-1} per year (assuming a baseline similar to the C stocked in the recently disturbed site following the last avalanche event). The maximum net biomass production for aspen is reported to occur after 18–32 years (Rytter and Stener, 2005). This reflects the very active juvenile growth during which the volume production per unit area of early-seral species such as aspen may exceed that of Norway spruce (*Picea abies*) (Børset, 1960). Starting at about 60 years of age, however, aspen ~~stands~~ gradually ~~to~~ reach a state of decline when mortality exceeds growth (Pothier et al., 2004). Therefore, when averaged over the entire life cycle, the more shade-tolerant Norway spruce allows for higher density and volume at similar site productivity indices (Børset, 1960). Light demanding aspen and shade-tolerant spruce may supplement each other, if they constitute separate overstory and understory, respectively (Langhammer, 1982). However, the stand will gradually develop along a successional process leading to dominance of the spruce–fir mixture, similarly to the control stand.

Areas damaged by stand-replacing disturbances usually act as carbon sources for some years (Thuille et al., 2000). In forest damaged by wind or avalanche, unlike wildfires, no CO_2 is directly released to the atmosphere during the disturbance event. However, even without consumption of organic matter (such as during wildfires) or removal by salvage logging or gravity (as may be the case of the recently disturbed site), the biomass transferred from live to dead pools is subject to microbial decomposition and quickly loses carbon while decomposing (Liu et al., 2011). Finally, the avalanche can remove soil carbon by mechanical elimination of the upper soil layers (Confortola et al., 2012; Korup and Rixen, 2014). However, in our study area the recently disturbed site preserved a significant amount of soil carbon (78 Mg ha^{-1} on average), most of which was stocked in soil. The lower C/N ratio in soils of the avalanche track indicated a higher fertility and slower C turnover, likely due to the prolonged permanence of snow and higher soil moisture.

We did not measure C fluxes, therefore the release of C from the recently disturbed site is unknown. More studies are needed to ascertain how much carbon is released following avalanche disturbances at the site and regional scale, and if and how long it takes for the post-disturbance vegetation to stock as much carbon as to equate the losses. The overall carbon balance can still be positive if losses in areas disturbed by avalanches are counteracted by mature and old-age forests serving as sinks in undisturbed areas between avalanche tracks.

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4.2. Plant diversity

Plant diversity has long been related to disturbance frequency and severity, i.e., in the framework of the (much debated) intermediate disturbance hypothesis (IDH) (Connell, 1978; Fox, 2013). In our study, we found that the active avalanche track had the highest species richness and diversity (Shannon index, although not significantly). This is in contrast with the IDH, but in accord with previous research on the effect of disturbances on plant diversity in mountain forests, and particularly avalanches (Fischer et al., 2012; Ilisson et al., 2006; Rixen et al., 2007).

The plant community of the avalanche track can be described as a true avalanche grassland (Erschbamer, 1989), with species belonging to typical avalanche grasslands (Molinio-Arrhenateretea) and to the adjacent mountain meadows (e.g., *T. flavescens*). High richness in the avalanche track can be explained by (1) gravitational transport of propagules of plants from higher elevations (Erschbamer, 1989); (2) increased habitat diversity due to the mosaic of areas with prolonged snow cover, eroded soil patches, or running melt water (Rixen and Brugger, 2004); (3) newly created forest edges (Duelli et al., 2002); (4) disturbance legacies (Franklin et al., 2002) such as coarse woody debris, pit-and-mound topography, and the mosaic of open areas and living legacies such as resprouting broadleaves (Rixen et al., 2007). Therefore, the maintenance of a periodically disturbed portion of the land is beneficial for overall species richness and diversity, facilitating the persistence of more light-demanding, early-seral species (Lonati et al., in press).

Previous research found that the shift from shrub- to tree- dominated vegetation occurred when the average interval between avalanches was 15 20 years (Johnson, 1987). Plant communities of the old disturbance and control sites were very similar, and shared many species from both the Piceetalia and the Fagetalia classes. Consistent with our study, previous research found that strong changes in species composition result from multiple avalanche occurrences, rather than single events that affect the forest structure heavily but may not result in sufficient changes in soil microclimate and mechanical disturbance (Fischer et al., 2012).

If we focus on the study site as a unique ecosystem, we notice that only one-third of the total number of species found was common to all disturbance treatments, i.e., the total species richness was higher than in any individual disturbance treatment. The mosaic of disturbed and undisturbed patches allows for coexistence of both early-seral, open-field species, and shade-tolerant species under or in the vicinity of the tree and shrub canopies. Further research is needed to ascertain if this diversity effects occur in other taxa, e.g., invertebrates, fungi, or lichens. Coarse wood debris, a commonly used metric of diversity for forest biota (Bouget and Duelli, 2004), was higher in the control forest than in the avalanche track; however, management in the former, and diversity of microsites in the latter, act as confounding variables, and could mitigate or even invert the simplistic relationship between disturbance frequency, CWD, and invertebrate diversity (e.g., Negro et al., 2014).

4.3. Ungulate habitat

As ungulates use resources very differently during the year, it is difficult to condensate habitat suitability in a single, static metric. We chose to use three different proxies for ungulate habitat: hiding cover, expressed as a function of tree density and size (Smith and Long, 1987); summer food availability, expressed by herb and shrub cover as a proxy (Moser et al., 2008), and winter food availability, expressed by measured browsing intensity on tree regeneration and shrubs. The use of browsing index alone would in fact underestimate habitat suitability of open areas dominated by herb cover such as those in or near the avalanche track.

Logically, herb and shrub cover was much more abundant in open, recently disturbed sites (Krojerová-Prokešová et al., 2010). However, ~~this~~ lacked the necessary hiding requirements due to low or non-existent tree cover, and was also less used during winter – probably due to scarce food and high snow cover. In fact, browsing on trees and shrubs was more severe in the control site – even if treatment effect was weak – probably due to the fact that distance between sampling plots was well within the daily movement capabilities of individual ungulates (Pépin et al., 2004). Browsing can affect future species composition of the forest (Motta, 1996); in the study area, this effect could be important for silver fir (Klopcic et al., 2010), which is highly palatable and, at the same time, not so abundant in the regeneration layer (Table 3).

In past studies, the optimal habitat for red deer and roe deer has been described as a mixture of open meadows and closed canopy, rich in forest edges so as to provide both food and shelter to the animals (Gill et al., 1996; Hanley, 1984; Licoppe, 2006). In areas hit by natural disturbance, coarse woody debris could also alter ungulate frequentation and feeding behavior. The effect of CWD on ungulate habitat use could be either positive – by stabilizing the snowpack, facilitating animal movement when snow is on the ground, or by the fact that saplings emerging from CWD are more readily visible to the deer (Pellerin et al., 2010) – or negative, if the abundance, size and spatial arrangement of CWD is such as to impair animal movement and feeding (de Chantal and Granström, 2007; Kupferschmid and Bugmann, 2005). We did not observe any site where this latter condition could be the case.

4.4. Protection from rockfall

Concerning protection against hazards, we assessed the effectiveness of the forest in stopping falling rocks of different sizes and preventing them from reaching the village and roads downslope (Fig. 1). The man-aged forest is currently effective against rockfall. In contrast, the (almost treeless) avalanche track is certainly not effective for rockfall protection, but any falling rock would be channeled within its steep banks and end up in the river below. The minimum required basal area for this slope is 20 m^2 ha^{-1} to reach a PRH of 95% for moderate sized rocks (RockforNET results). In the recent disturbance site, or in the eventuality of a new avalanche event as severe as the 1959 one, actions to mitigate the rockfall hazard should be carried out if the rockfall protection service is prioritized (e.g., rockfall nets or temporary log fences).

More interestingly, the old disturbance stand is currently very effective against rockfall protection (PRH: 99% for moderate-sized rocks, and 83% for large rocks), mainly because of the high density of stems, which may act as a fence blocking falling rocks (Gsteiger, 1993; Jancke et al., 2009; Vacchiano et al., 2008).

5. Conclusions

In order to maintain or replenish the provision of ecosystem services in the face of natural disturbances, managers need to understand the relationship between disturbance frequency, intensity, and the duration and magnitude of the consequent changes in ecosystem service provision.

This study assessed changes in ecosystem services provided by a spruce–fir mountain forest disturbed by avalanches, by comparing carbon stock, plant diversity, ungulate habitat, and protection against rockfall in stands experiencing zero, one, and multiple disturbance events. We showed that: (1) high disturbance frequencies are beneficial for plant diversity, (2) after 50 years the forest was optimal for rockfall protection, and (3) the regularly managed forest had the highest carbon stocks.

Avalanches are a source of patchiness and habitat heterogeneity. Once safety of households and roads is ensured, the maintenance of a share of the landscape disturbed by avalanches of variable size, magnitude and frequency can be beneficial to several ecosystem services, such as biodiversity and wildlife habitat. Carbon losses due to disturbances can be offset by enhanced conservation of mature and old-aged forests

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in undisturbed areas. Elucidating tradeoffs between ecosystem service provision and disturbance frequency will help managers in planning management actions (e.g., avalanche suppression) and distribute them across the landscape according to the ecosystem services to prioritize.

6. Uncited reference

Motta and Edouard, 2005

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.coldregions.2015.03.004. These data include Google maps of the most important areas described in this article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.coldregions.2015.03.004.

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